

IX.—*The Development of the Sea-Anemones Metridium dianthus (ELLIS) and Adamsia palliata (BOHAD).*

By JAMES F. GEMMILL, *M.A., M.D., D.Sc.*

Communicated by Prof. E. W. MACBRIDE, F.R.S.

(Received May 17, 1918,—Read June 27, 1918.)

[PLATES 58–60.]

CONTENTS.

	PAGE
I. <i>Metridium</i>	351
II. <i>Adamsia</i>	355
III. Discussion	359
IV. Abnormalities	366
V. Summary	367
References	368
Explanation of Plates	370

Metridium and *Adamsia* are genera of the Family Sagartiadæ, Sub-Order Malacactineæ, Order Actiniidæ, Sub-Class Zoantharia. The Malacactineæ (or “True” Sea-Anemones) with the Scleractineæ (or “True” Corals) make up the Order Actiniidæ. In this Order there is an eight-mesenteried Edwardsia stage, and thereafter a primary cycle of six couples of mesenteries is (or may be inferred to be) completed by the addition of two pairs to the eight Edwardsia mesenteries, while succeeding cycles are formed in the exocoelæ of the pre-existing mesenterial cycles.* Other so-called sea-anemones are the Zoanthidea and Cerianthidea, but, from the arrangement of their mesenteries, they have to be classed as separate Orders, though in all of them the primary Edwardsia mesenteries can be recognised during development or in the adult condition. The remaining Zoantharian Order, the Antipathidæ, is somewhat aberrant. Their development is unknown, but it is stated that one species, *Leiopathes glaberrima*, shows distinct indications of an Edwardsia stage.

I. METRIDIDIUM† (Plate 58, figs. 1–24).

In this genus the column is long, cylindrical, smooth, naked, pierced by cinclides and ending in a capitulum which is divided into lobes and carries numerous short

* See BOURNE, 3, p. 104.

† The generic name *Metridium* due to OKEN is synonymous with, but has priority over, *Actinoloba* due to BLAINVILLE.

tentacles. A ring-like thickening surrounds the column below the capitulum. The sexes are separate and indistinguishable externally.

Having ascertained by microscopical examination that the ovaries of *M. dianthus* were full of *unripe* eggs in April, I made the necessary arrangements for stocking some of the research tanks at the Millport Biological Station with full-sized specimens from the piles at Kepeel Pier, a short distance from the station. Two well-marked varieties occur together there, one flesh-coloured and the other white. A tank was reserved for each and two other tanks for crosses. As the eggs promised to be small even when full-grown, the outflow from each tank was drawn through a large fine-meshed filter-drum immersed in the tank, so that they might not be swept away unobserved.

The first *spawning* was noted on June 5. The eggs proved to be heavier than water, and sank to the bottom, where they were seen without difficulty in contrast to the white glazing of the tanks. Filter-drums were accordingly unnecessary at this stage. The eggs are opaque, 0.1 mm. in diameter, dark greyish-green in the white variety and brick red in the other. Development is the same in both.

Natural *fertilisation* readily occurred, a mutual stimulus to spawning being no doubt communicated by the sexual products. The same individuals spawned several times at longer or shorter intervals (2-10 days), and the last batches of eggs were extruded on July 10. I am much indebted to Mr. John Peden, laboratory attendant at the station, for helpful care in stocking the tanks, attending to eggs and larvæ, and preserving a full series of stages.

When spawning the anemones are usually well expanded, the stomodæum being partly everted and elongated in the axis of the siphonoglyphs. The eggs emerge not from the siphonoglyphs, but along the sides of the stomodæal aperture, being slowly swept out as if by the action of cilia there. (The cilia on the sides of the stomodæum act at times, if not continuously, as sweepers-out of the stomodæal cavity, cf. CARLGREN, 5.) The eggs are usually discrete from the first, but may be entangled for a time in fine strands of mucus, which soon dissolve away. *Maturation* appears to be advanced or completed just at the time of spawning, as none of the freshly-spawned eggs showed a germinal vesicle, while teased-out ovaries from resting specimens during the spawning season showed numberless full-sized ova, all with large germinal vesicles.

The ripe nucleus is invisible in the opaque egg-mass, but cleared specimens and sections show that it lies excentrically at a point about a third of the diameter of the egg inwards from the surface. The egg membrane is very thin, closely adherent, and unprovided with spines or other surface markings, or with a micropyle. The egg substance is finely granular, the granules being practically uniform in size and distribution, leaving only a very narrow clearer rind at the periphery.

Equal or subequal *segmentation* occurs. There is a tendency in some eggs for the inner ends of the daughter-cells to remain unseparated for a time, and in others for

the superficial furrows to be shallow and indistinct. Figs. 2, 3, 5 are photographs of typical stages showing complete segmentation.

A small central cavity appears at the 16-celled or even an earlier stage. As segmentation proceeds the cavity enlarges, sometimes directly and sometimes after preliminary formation of foldings of the blastula-wall (*cf.* pp. 356 and 360), which afterwards straighten out. The *blastula* cavities in the best broods (Plate 58, figs. 7, 9, 10) are devoid of other than fluid contents, but sometimes they contain cellular and non-cellular materials (Plate 58, fig. 8; Plate 58, fig. 20). In the best broods the wall of the blastula is formed of a single layer of cells, having the nuclei and most of the protoplasm near the surface, while the inner ends of the cells are yolky in character (*cf.* HAMMAR, 15). The cellular material above referred to includes segmentation cells, which have failed to arrange themselves alongside their neighbours in the blastula wall, and which may proliferate, while the non-cellular material consists of the inner yolky ends of blastula wall cells which have been constricted off (*cf.* *Adamsia*, p. 356).

The blastula begins to elongate in the future oral-aboral axis. From the first, the cells to one side of the segmenting mass have been slightly larger than the rest, and these cells now form a thickened patch at what will be the oral end. The end in question flattens and pushes inwards near its middle part, the larvæ becoming somewhat conical in shape. This marks the beginning of *gastrulation*. By further in-pushing (Plate 58, figs. 11–13) the gastrula stage is reached, the blastopore being now nearly, but not quite, in the middle of the somewhat truncated oral end. The blastopore has also become slightly elongated, one end (the future sulcar end, pp. 355, 363) being somewhat nearer the aboral pole than the other (*cf.* Plate 58, figs. 10, 13, 15). The former end has usually a less prominent lip or margin than the latter. In the earliest stages of gastrulation there is often cell-proliferation on the inner aspect of the in-pushing area, producing a small cap of additional endoderm, into which the archenteric cavity soon extends.

A short *stomodæum* is produced by early involution at the blastopore. It lengthens afterwards, mainly by interstitial growth. It shares in the elongation of the blastopore above described. Its cells may be distinguished from those of the archenteron by being closer set and more columnar, and by having longer and more deeply-staining nuclei. The archenteron cells form a less regular layer.

Also at the commencement of gastrulation some branched cells resembling "mesoderm" cells are given off from the endoderm into the blastocœle. A few flattened "mesodermal" cells are found later between ectoderm and endoderm.

Swarming begins in the early blastula stage, the movements being at first irregular but afterwards causing progression with the pointed (future aboral) end in front, together with rotation in the contra-solar direction, as viewed from that end. These movements persist through the planula stage, into which the late gastrula passes insensibly. Further elongation occurs: the shape becomes more cylindrical,

and the archenteron larger, while the blastula cavity is obliterated by approximation of hypoblast to epiblast. The stomodæum becomes longer.

The first two *mesenteries*, the future sulco-laterals (or ventro-laterals of authors) appear far ahead of the others, growing aboral-wards, each carrying on its free edge an extension of the stomodæal epiblast for the developing mesenteric filament. *Stinging cells* appear in the early planula, chiefly at its oral and aboral ends. Various acids readily cause extension of the stinging threads. (Plate 58, fig. 17.)

Towards the end of gastrulation a tuft of six or seven long rather stiff cilia grows out at the apex of the aboral pole from a small group of elongated columnar cells, and these cilia form a striking feature throughout the planula stage (*cf.* Plate 58, figs. 15, 22). When stretched out the cilia are half as long as the larva itself. They lie close together and are sometimes held straight, sometimes curving to one side or the other, as the larva progresses. Should the cilia encounter any obstacle, the larva quickly swerves. In the later stages the cells which carry the cilia sink slightly inwards, forming a small aboral pit, underneath which are a few branched cells. No doubt the whole forms an *aboral sensory* organ. CARLGREN's (6) figure of the late planula of *Sagartia viduata* agrees with the above description. He adds that *Sagartia viduata*, *S. undata*, *S. troglodytes* and *Metridium dianthus* have practically identical larvæ.

Reference should also be made here to the aboral nervous elements described by McMURRICH in *Rhodactis sancti-thomæ* (24), APPELLÖF (1) in *Actinia mesembryanthemum* and DUERDEN (9) in various Scleractinian larvæ and in *Lebrunia*.

The blastopore and stomodæal canal are not sealed up even temporarily, and indeed in the late planula are often opened as the creature swims along. *Ciliary feeding* occurs at this period. Foreign particles may be seen in the archenteron, and slight, though not great, increase of size occurs. Fine carmine grains are readily ingested. CARLGREN (5) has shown that ciliary feeding almost certainly occurs in various adult Malacactineæ and in the Zoanthidea.

The gastrulæ and young planulæ swarm freely at all levels in the hatching vessels and will be swept away if there is a through circulation of water. The use of filter drums now becomes necessary in such vessels, but it is simpler to pipette the larvæ out into shallow separate dishes under aëration, and to change the water by pipetting them again into new dishes at intervals of a few days.

Older planulæ tend to remain at the bottom, moving horizontally and remaining stationary from time to time. Many of these now become temporarily *attached* to the bottom, *mouth downwards* (*cf.* Plate 58, fig. 24), the stomodæal canal everting itself to a varying extent and forming a sucker surface, now smaller now larger, permitting slow creeping movements to take place. I think it extremely probable that the larva is now feeding on such organic material as may be attached to the substratum.

Unfortunately I had to leave Glasgow in the beginning of July, just at the time

when the above stage was reached in my cultures, and on my return after some weeks the larvæ had disappeared, so I am unable to say how long the stage of creeping on the mouth may last, or to describe aboral fixation.

The sulco-lateral mesenteries early become edged by down-growths of stomodæal ectoderm, for the *mesenteric filaments*. These are ciliated in the larva but I could not make out in what direction the cilia work. However, in the smallest attached specimens of *Metridium* obtainable from the shore there is an aboral-ward current along the free borders of the mesenteries, and an oral-ward current along the outer walls of the gastro-vascular pouches. The early development and large size of the sulco-lateral mesenteries and their filaments suggest a comparison, from the physiological point of view, with the aboral ciliated bands which one finds in echinoderm and other larvæ, while the extension of ectoderm over endoderm which occurs in their formation is also paralleled in echinoderm development (see also p. 364).

In my latest larvæ, slight folds of hypoblast could be recognised near the oral end, foreshadowing the formation of the sulculo-lateral, sulcar, and sulcular mesenteries. Of these, so far as I could judge, the sulculo-laterals appear first, the sulcars next, and the sulculars a little later.

I have not been able to relate from direct observation the early somewhat excentric situation and the slit-like shape of the blastopore to the position of particular mesenteries, but as APPELLÖF (1) pointed out, this may be done with the help of LACAZE DUTHIERS' data for *Actinia mesembryanthemum*, the conclusion being that the shortest meridional line in the larva is at the future sulcar side (see p. 363). DUERDEN (9) notes also that in Scleractinian larvæ the blastopore has a slightly excentric position.

II. ADAMSIA PALLIATA (Plates 59, 60, figs. 25-71).

The genus *Adamsia* belongs to the same family (Sagartiadæ) as *Metridium* (see p. 351). The characters of the genus are . . . all attached to movable objects: one or two girdles of cinclides on the column, each cinclide piercing a small tubercle: rest of column smooth: base secreting a cuticular membrane: a well-marked sphincter present: tentacles numerous.

The sexes are separate, and *spawning* in the Firth of Clyde lasts throughout September and the early part of October. Males and females are found in approximately equal numbers. Natural fertilisation regularly occurs, a mutual stimulus to spawning being evidently operative, as in *Metridium*. The eggs are usually shed about midnight, but more timely spawning may be induced if the tanks are closely covered up to exclude all light in the early afternoon. This was done in order to secure quite freshly-spawned eggs at an hour more suitable for observing the earliest stages of development. Ripe males and females may, with difficulty, be distinguished from one another by taking the specimens out of water and noting the somewhat larger ridges caused by the fertile mesenteries on the surface of the female

in the collapsed condition. The same individuals spawn several times in each season. The Millport records show that spawning may also occur in early spring.

Maturation must take place immediately prior to spawning. Sections of ovaries with full-sized ova, even during the spawning season, show practically all the eggs still with a large germinal vesicle.

The eggs being somewhat lighter than water tend to float. They are opaque, spherical, 0.25 mm. in diameter. They vary as regards colour in different individuals from brick red to yellow, yellowish-white, and white. The last two-named varieties have a peculiar glistening appearance. The ripe nucleus is invisible in the egg mass, but may be found in serial sections lying excentrically as in *Metridium* (p. 352). The great mass of the egg is made up of small yolk granules which are almost uniformly distributed, though not quite so closely packed near the centre of the egg. The egg membrane is thin, closely adherent, and unprovided with spines. Underneath it is an extremely narrow zone relatively free from granules (Plate 59, fig. 48).

After fertilisation the segmentation *nucleus divides* into two daughter nuclei, which in turn divide. Only when this second division is nearly complete is there the slightest indication of a commencing division of the egg mass into two by a cell wall beginning to form in the plane perpendicular to the axis of the first spindle. Immediately thereafter the second division of the cell mass can be noted as commencing, but the first and second *cell divisions* are completed at practically the same time, so that the first stage of external segmentation is the four-celled one. In this stage, the cells are equal in size and lie in one plane, their apposed surface being flattened against one another. An eight-celled stage supervenes, in which typically at first each cell lies directly against its sister-cell, so that the whole mass is quadrangular, but re-arrangement into the less regular grouping soon takes place. Four of the cells on one side of the mass are usually a little larger than the corresponding four on the other.

The succeeding divisions are sub-equal but irregular, giving rise to a *morula* which though at first roughly spherical in shape soon becomes extremely distorted by the formation of surface folds and ridges, always with a tendency to flattening in one plane. This may be called the *pre-blastula* stage (Plate 59, figs. 28-31; Plate 59, figs. 49-51).

Meantime, an irregular central cavity has appeared containing fine granules extruded from the cells (Plate 59, fig. 57). The result is to produce a thinnish crumpled disc made up of two sheets of cells separated by the cavity in question, which, however, is frequently of minute size. The crumpled disc gradually changes to a saucer-like shape by smoothing of the minor furrows and folding of the edges towards one side (Plate 59, fig. 32; Plate 59, figs. 52, 53). The saucer in turn becomes less spread out, but thicker-walled, and the cavity of the saucer gradually fills out, remaining, however, as a small dimple for a time (Plate 59, figs. 54, 55). Meantime, cell division has continued, the nuclei keeping near the external surface of the mass. The inner ends of the cells became prolonged as non-nucleated vesicles

surrounded by a protoplasmic wall and form a central reticulum of "*trophenchyme*" (Plate 59, figs. 55-58).

The full *blastula* stage is reached by smoothing out of the last remains of the hollow of the cup, and commencing elongation. The shape is now oval, and one end, the end at which gastrulation will take place, soon becomes rather broader than the other. In the best broods the central reticulum is entirely devoid of nuclei, but in other cases nuclei may be present in larger or smaller numbers (Plate 59, fig. 56), and when present are derivatives of ectodermal cells at the bottom of a fold or of the saucer cavity, which did not succeed in ranging themselves with the rest on the outer surface. They are not the regular endodermal cells, and as far as I could judge are destined to break down and disappear, partly *in situ* and partly within the archenteric cavity, into which many pass later along with the central trophic material (trophenchyme) of the blastula (see below). Such relatively late stages as are illustrated in Plate 60, figs. 63-68, often show degenerating nuclei within the stomach cavity.

Gastrulation begins at the broad end of the larva (Plate 59, figs. 36-42, and Plate 59, figs. 60-62). This end becomes flattened, then pitted inwards, not in the middle, but usually a little to one side, so that the opening has a prominent lip opposite a retreating one (Plate 59, figs. 36-37). As in *Metridium* (p. 353) the blastopore is slightly elongated between the two lips named. The blastopore usually, but not always, coincides with the position of the former saucer opening. During the progress of gastrulation the central trophic material of the blastula gradually finds its way through the inpushing endoderm into the archenteron, which, in later stages, it fills with a loose reticulum often showing small nuclei in course of degeneration.

In view of the data given in the preceding paragraphs, I venture to suggest that in general the cell-contents of solid coelenterate planulae with endoderm already formed need not be considered as wholly endodermal, but that part is a modified mesenchyme having a diffuse origin, and now "trophenchymal" in character. For a suggested explanation of its presence, see p. 365.

In some *Adamsia* larvæ the endoderm has to be described as arising partly by *unipolar* proliferation. The invaginating area becomes capped by a thicker or thinner mass of endoderm proliferated from its apex, and the archenteron extends into the middle of this mass, giving rise to the deepest portion of the gastric cavity. Whether any "mesoderm"* arises from endoderm during gastrulation proved impossible to decide.

A short *stomodæum* arises by involution at the blastopore, before gastrulation is completed, and subsequently increases in length by interstitial growth.

Cilia appears on the early blastula. At first it moves about irregularly, but when

* "Mesoderm" is used here, and on p. 353, to indicate middle layer cells proliferated from endoderm in the course of gastrulation.

elongation takes place the movement is a progression with the pointed (future aboral) end in front, combined with rotation in the sinistral or contrasolar direction. There is no special tuft of elongated cilia at the aboral end such as forms so marked a feature in the planula of *Metridium*. The gastrulæ and young planulæ tend to swim near the surface, but the older larvæ are found for the most part moving horizontally along the bottom of the hatching vessel, from time to time making upward excursions and then sinking down again. They are markedly elongated in the oral-aboral direction, and cleared specimens begin to show traces of the *mesenteric septa*, especially of the sulco-laterals (Plate 59, figs. 44-45).

Serial sections make it clear that of the eight primary mesenteries the two sulco-laterals are the first to appear, and for a long time are much the largest (*cf.* Plate 60, figs. 68, 71). They carry on their free surface a ridge of columnar ciliated cells for the future mesenteric *filament* which as in *Metridium* is a downward growth from the stomodæum (*cf.* Plate 60, figs. 64, 66, 67), and in the late larva extends to within a third of the length of the larvæ from the apex. The other mesenteries appear practically together, though it seemed that the sulcars (or ventrals of authors) and the sulculars (or dorsals of authors) were slightly later than the sulculo-laterals (*cf.* Plate 60, figs. 70-71). *Stinging cells* are already present over the larva as in *Metridium* (p. 354), but their distribution is more uniform.

The larva has now considerable power of elongation and contraction. *Fixation* by the aboral end next takes place, the larvæ being at first anchored loosely so that they can be detached by a current from a pipette. Soon, however, the attachment is firm and definite. This attachment must be by cement formation since there is no sucker to which it might be due. Fixation is followed by the throwing out of the eight *tentacles* (Plate 59, fig. 47), each corresponding to an intermesenteric space. These tentacles are not at first all of the same size. The four largest correspond respectively with the spaces between (*a*) the two sulcular mesenteries, (*b*) the two sulcars, (*c*) two laterals on either side. The smallest tentacles are the two between the sulculo-laterals and the sulculars.

Soon after attachment the *mouth* opens freely, and the body of the young anemone becomes elongated and cylindrical. It is still semi-transparent, allowing the ciliary currents inside to be watched. These are aboral-wards along the borders of the mesenteric septa and oral-wards along the sides and bottom of the inter-mesenteric spaces.

I failed to rear the anemones to further stages, and though they survived for several months, there was no great increase in size, and no new mesenteries or tentacles were formed. In fixation the larvæ attached themselves to glass, large sand grains, or small stones, but preference was given to fragments of dead mollusc shells, though not to shells carried about by tiny hermit crabs.

III. DISCUSSION.

- (a) Ova, segmentation, blastula formation, p. 359.
- (b) Origin of endoderm, p. 361.
- (c) Formation of mesenteries and mesenteric filaments, p. 362.
- (d) Phylogeny, p. 363.

(a) *Ova*, etc.—It may be of interest to bring together briefly such data regarding the eggs and early development of Malacactineæ as I can gather from the literature at my disposal or supply from observation.

Size of ova.—*Metridium dianthus*, 0.1 mm. in diameter; *Sagartia troglodytes*, 0.1 mm.; *Metridium marginatum* (McMURRICH, 24), 0.1 mm.; *Adamsia palliata*, 0.25 mm.; *Urticina crassicornis*, 0.6 mm.; *Bolocera tuedia*, about 1.1 mm.; *Peachia hastata*, judging from a figure by FAUROT (10), 0.25 mm.; *Anthea cereus*, 0.35 mm. It will be seen that the largest eggs in the list (those of *Bolocera*) have more than 1000 times the capacity of the smallest (those of *Metridium*).

Egg membrane.—Smooth in *Metridium dianthus*, and *M. marginatum* (McMURRICH, 24), *Adamsia palliata*, *Sagartia troglodytes*: with characteristic spines in *Urticina* (APPELLÖF, 1), *Peachia* (FAUROT, 10), *Actinia mesembryanthemum* (LACAZE DUTHIERS, 19), *Bolocera tuedia*, and *Anthea cereus*.

Cell contents.—Finely granular with practically uniform distribution of granules, *Metridium dianthus*, and *M. marginatum* (McMURRICH, 24), *Adamsia*: granular with the granules distributed in zones and mixed with clear vesicles most abundant centrally, *Urticina crassicornis* (APPELLÖF, 1), *Bolocera tuedia*.

Micropyle.—Present in *Urticina*: absent in *Metridium dianthus*, and *M. marginatum* (McMURRICH, 24), and *Adamsia*.

Segmentation.—Equal or subequal segmentation is the rule. The segmentation is total from the first in *Metridium dianthus*, and *M. marginatum* (McMURRICH, 24), *Peachia* (FAUROT, 10), *Sagartia parasitica* (KOWALEWSKY, 18, and FAUROT, 10), *Actinia bermudensis* (CARY, 7), *Cerianthus*.* Cleavage of the cell mass is delayed till after more than two daughter nuclei have risen from the segmentation nucleus (four in *Adamsia*, sixteen in *Urticina crassicornis* (APPELLÖF, 1), more than sixteen in *Bolocera tuedia*. It should be added that, in *Adamsia*, APPELLÖF (1) and FAUROT (10) speak of the occurrence of a two-celled stage, but such a stage is entirely exceptional in my experience. It may be noted that, among Alcyonarians, the eggs of *Alcyonium digitatum* undergo total cleavage from the first (MATTHEWS, 29), while those of *Renilla* (WILSON, 34) take the course characteristic of *Urticina* and the Arthropods. McMURRICH describes secondary loss of cell partitions as sometimes occurring in *Metridium marginatum* (24). I have not been able to satisfy myself that this takes place in *M. dianthus*, but, on the other hand, it

* See DELAGE (8), p. 676.

is not uncommon, though atypical, for the early divisions to be incomplete, and to leave the inner ends of the cells confluent (*cf.* Plate 58, fig. 6).

Blastula formation.—Blastula formation is at its simplest in *Metridium*, following the course taken, for example, by the developing eggs of an ordinary sea-urchin (*Echinus esculentus*) or starfish (*Asterias rubens*). However, in *Metridium* the yolk of the blastosphere cells is aggregated towards their inner ends, and there is a tendency in atypical cases for the yolky parts to become separated off as non-nucleated fragments into the central cavity, as well as for nucleated cells derived from the original morula mass to be present there and to proliferate. Similar cells are frequently found in the central cavity of abnormally developing sea-urchin and starfish blastulæ. As in *Metridium*, they are not concerned with the formation of the proper endoderm, but ultimately break down and are absorbed, unless they are present in sufficient quantity to interfere with the growth and differentiation of the larvæ. The occurrence of analogous cells in the central trophic reticulum was sometimes noted in *Adamsia*, where they were found in greatest numbers just internal to pre-blastula folds, and, in particular, to the remnant of the saucer opening.

Adamsia exhibits in a most striking manner these peculiar *foldings* of the pre-blastula, which have now been found to precede the full blastula stage in many different forms, *e.g.*, *Cribrella* (MASTERMAN, 27), *Solaster* (GEMMILL, 11), *Porania* (GEMMILL, 12), *Luidia* (MORTENSEN, 30), *Cucumaria* (NEWTN, 31), *Alcyonium* (MATTHEWS, 29), and, in a minor degree, *Metridium*. Such foldings were already noted in *Adamsia* by FAUROT (10), and we may infer from a remark by this author that they are characteristic of *Cerianthus* as well. They are not referred to by APPELLÖF (1) in his description of the development of *Urticina crassicornis*, but I find that they occur very markedly in this species, as well as in *Bolocera tuedia*. It is a curious circumstance that the *Adamsia* pre-blastulæ commonly take on a saucer or cup-like shape during the stage in question. Probably the cause is a mechanical one, depending on the interaction of two processes, *viz.*, the straightening out of the pre-blastula folds and the separation of the central trophic reticulum described on p. 357 and referred to below.

Formation of central trophic mass.—APPELLÖF, in *Urticina* (1), first gave an adequate description of the manner in which this mass arises, namely, by constriction of the inner, usually non-nucleated ends of the cells of the morula and pre-blastula. In the immediately succeeding stage this author shows the blastosphere cells definitely separated off from the central mass. The feature in question is not found in *Adamsia*, where the inner ends of the blastosphere cells remain continuous with the strands of the central reticulum till near the end of gastrulation. Probably the formation in the blastula of a non-nucleated or sparsely nucleated trophic central mass is a characteristic feature of Actinian development, except in such species as *Metridium dianthus* and *marginatum*, where the eggs are minute and

have little yolk. At any rate, we have now detailed accounts of the origin of the central trophic mass in *Urticina* and *Adamsia*, and, from the descriptions of FAUROT (10), KOWALEWSKY (18), and APPELLÖF (1), we can infer the likelihood of similar processes occurring in *Adamsia parasitica*, *Peachia hastata*, *Cerianthus*, *Bunodes*, and *Actinia mesembryanthemum*. They occur markedly in *Bolocera tuedia*. A phylogenetic explanation is suggested on p. 365.

(b) *Endoderm Formation*.—Both in *Metridium* and *Adamsia* the endoderm arises by invagination, sometimes accompanied by unipolar cell proliferation, and the developing archenteron is hollow. In *Metridium*, the blastula cavity being empty, the process is uncomplicated. In *Adamsia* the in-pushing endoderm allows the central mass to pass gradually through into the archenteric cavity, without losing continuity as a layer. APPELLÖF (1) was the first to describe this process in Actinian development (*Urticina crassicornis*).

I am unable to accept McMURRICH'S conclusion (26) that endoderm formation takes place by delamination in *Metridium marginatum*. This species is closely allied to *M. dianthus*, with which it agrees in the general character of the ova and in the details of segmentation and blastula formation. McMURRICH'S description and figures do not testify to the presence of nuclei in those portions of the blastosphere cells which he believes are separated off to produce the hypoblast. His view is based rather on not having secured evidence of invagination than on having secured evidence of delamination. I can only infer that his material was deficient in the early stages of gastrulation, and possibly also that some of it showed the abnormal features referred to on p. 353, and illustrated in Plate 58, figs. 20, 21, of this paper.

We can now say with some confidence that gastrulation is the general rule in Malacactinian development. Apart from *Metridium* and *Adamsia*, it has been described in *Urticina* (1), and *Actinia bermudensis* (CARY, 7), *Actinia mesembryanthemum* (JOURDAN, 17), *Cerianthus*, and an Actinian allied to *A. mesembryanthemum* (KOWALEWSKY, 18). To these I am now able to add *Bolocera tuedia*. The case appears to be different in Alcyonarians, where delamination is described by WILSON (34) in *Renilla* and MATTHEWS (29) in *Alcyonium digitatum*. Again, in the Scleractinian *Manicina*, WILSON (35) states that transverse division of the blastosphere cells takes place, giving rise to a coarsely granular endoderm, but this is very like the mode of formation of the central trophic mass in Malacactineæ.

Embolic gastrulation, which occurs also in the Scyphozoa, is almost certainly the type from which such modes of endoderm formation as epibole in Siphonophores and Ctenophores, and unipolar immigration in various Hydromedusæ, are proximately derived. However, in view of the "regulatory" potencies exhibited by the blastomeres and blastula-fragments of *Adamsia*,* it seems entirely probable that cells proliferated or nipped off into the interior, normally or pathologically, from any

* See p. 366 and cf. ZOJA'S (36) results for various Hydromedusæ.

part of the blastula surface, will strive to become endodermal *in functional imitation of* invagination endoderm, and, under suitable circumstances, may succeed. Experimental embryology shows that potencies of structure-formation which, under normal circumstances, have been acquired and are exercised only locally, may become part and parcel of the heredity of the whole layer to which the structure belongs. Witness lens formation on the skin of amphibian larvæ over transplanted optic vesicles.

Supplementing or supplanting of gastrulation-endoderm by endoderm of multipolar or of diffuse ingression origin might thus gradually take place in the history of particular stocks, families, and even genera. It involves no inconsistency to hold that gastrulation is the primary method of endoderm formation in coelenterates, and yet to recognise that the other methods named have become fixed as normal for particular forms. Surely the *polarity* between ectoderm and endoderm could never have been established except through the formation of a digestive cavity, which sank in from the surface, and opened on the surface from the first.

(c) *Formation of mesenteries*.—It has long been recognised that a stage with eight primary mesenteries (Edwardsia stage) in characteristic bilateral symmetry, forms an important landmark in Zoantharian growth. *Metridium* and *Adamsia* furnish additional illustrations of the definiteness of this stage. In *Metridium* the two sulco-lateral (or “ventro-lateral” of authors) mesenteries appear far ahead of the others, and they have probably a current-producing function in the late larva (p. 354). The same pair has a similar but less marked priority of origin in *Adamsia*. LACAZE DUTHIERS (19) in *Actinia mesembryanthemum*, FAUROT (10) in *Halcampa*, and McMURRICH (24) in *Rhodactis sancti-thomæ* and DUERDEN (9) in Scleractinian larvæ also describe the sulco-laterals as being the first to appear.

In *Metridium* the sulculo-laterals next become evident. Then follow the sulcars (ventrals of authors), and the sulculars (dorsals of authors), the latter, as far as I could judge being slightly later than the former. This is the sequence described by McMURRICH (24) for *Rhodactis sancti-thomæ*, and by FAUROT (10) for *Halcampa*, but LACAZE DUTHIERS (19) in *Actinia mesembryanthemum* gives the sulculars as second, the sulcars as third, and the sulculo-laterals as last in the order of appearance, though as Haddon suggests, his work needs revision by serial section methods. *Adamsia* seems to agree with *Metridium*, *Rhodactis*, etc., though there is little difference as regards the three pairs of mesenteries in question. In the heavily yolked eggs of *Urticina*, with presumably abbreviated development, APPELLÖF (1) described the eight mesenteries as arising at much the same time or without regular sequence, though the sulco-laterals seemed to show a certain priority. I can add that this priority is definite in *Urticina crassicornis* at Millport, and that the sulculars are the last to be formed.

The primary gastro-vascular pouches are naturally eight in number, and two of them, the sulcar and the sulcular, lie in the axis of bilateral symmetry. The eight

first tentacles correspond in position with the pouches. In the Scleractinians (DUERDEN 9, WILSON 35, and others) the eight primary mesenteries arise in the same order as in *Metridium* and *Rhodactis*.

The evidence from *Metridium* and *Adamsia* appears quite definite that the mesenteric *filaments* consist of (or at any rate include) a stomodæal epiblastic down-growth in the case of the sulco-laterals. Probably the same thing is true as regards the other mesenteries, though their filaments had not yet developed in my oldest specimens. This agrees with the general trend of recent evidence on the question in the *Actiniidæ*.

(d) *Phylogeny*.—Whatever may be conjectured about the primitive coelenterate planula, the balance of embryological evidence tends to show that the *intermediate* planula for Scyphozoa and Anthozoa, was a hollow free-swimming digestive bag with a single opening—originally the blastopore of an embolic gastrula—and a tendency to the formation of radially arranged mesenteries and gastric pouches.

I venture to suggest that while the Scyphozoa remained essentially free swimming, except for purposes of asexual reproduction, and preserved or perfected their radial symmetry, the Anthozoa (as well as the Turbellarians, and probably also the higher Metazoa) had, as their *proximate* ancestral form, a larva which took to creeping mouth downwards and gathering food material from the substratum, thereby acquiring an ectodermal stomodæum for the ingestion of food, and increasing their mesenchyme for body movements. If the larva took to moving in a particular direction the mouth might naturally become elongated in that direction and other rudiments of bilateral symmetry be acquired. The aboral sense-organ would also shift forward. Hints of this stage may be seen in the slit-like character and excentric position of the blastopore in Actinian larvæ (p. 355), one end of the slit being nearer the aboral pole than the other. That nearest the aboral pole would naturally mark the "head" end of the creeping planula. Similar features carried afterwards to full bilaterality and principal-axis formation are recognised as occurring in Turbellarian ontogeny (LANG, 20).

As regards the Zoantharia it appears to me legitimate on these lines to amplify for the *Edwardsia* stage the suggestion (made by VAN BENEDEN (2) for *Cerianthus*) that the arrangement of the gastro-vascular pouches corresponds with the arrangement of the *cœlomic pouches* in the higher segmented forward-moving animals. This view takes, as necessary foundations, SEDGWICK'S (33) well-known homology between gastro-vascular pouches and endodermal cœlomic outgrowths, and his comparison of mouth and anus with the two ends of an elongated primitive mouth, the middle part of which became closed.

As APPELLÖF (1) pointed out in the case of *Urticina*, it would appear from a comparison of Actinian larvæ with the early growth stages of *Actinia mesembryanthemum* described by LACAZE DUTHIERS (19), that what is called above the "head" end of the blastopore opening is to be identified with the sulcar side

of the Actinian stomodæum. We may accordingly institute the following comparison of the gastro-vascular pouches in the Edwardsia stage common to all Zoantharia ; (1) The sulcar pouch corresponds with an (unpaired) præoral cœlomic cavity ; (2) the pouch on either side between the sulcar directive mesenteries and the sulco-laterals with a (paired) collar cœlomic cavity ; (3) that on either side between the sulco-laterals and the sulculo-laterals with a (paired) first trunk cœlomic cavity ; (4) that between the sulculo-laterals and the sulcular directives with a (paired) second trunk cœlomic cavity ; and (5) that between the sulcular directives with a third (unpaired) posterior trunk cœlomic cavity.

The comparison ceases here for most of the Zoantharia, since after the Edwardsia stage, increase in the number of pouches takes place by subdivision of already existing ones. However, in *Cerianthus* if, as seems certain, the orientation given by VAN BENEDEN (1), DELAGE (8), FAUROT (10), BOVERI (4), and McMURRICH (26) be right, there is, as VAN BENEDEN (2) pointed out, continuous production of new pouches at the sulcular or "posterior" end, thus providing a striking resemblance to cœlom formation in such an animal as *Amphioxus*.

The sulco-lateral mesenteries of the late Actinian larva (*cf.* Plate 58, figs. 18–19) divide the archenteron into a smaller cavity (on the sulcar side) which may be taken as representing the "anterior" pouch of the hypothetical tetramerous cœlenterate ancestor (MASTERMAN, 27) and a larger cavity (on the sulcular side) which will represent for a time the other three pouches of the ancestor. Assuming that the primitive cœlenterate mouth lengthened and closed medially to form the definitive mouth and anus, the sulco-lateral representatives would probably be found commencing in the floor of the mouth much in the position of the *endostyle rudiment* of *Amphioxus** and Tunicates, and of the ventral ciliated band of *Tornaria*, and of the V-shaped part of the adoral ciliation in echinoderm larvæ.

These structures are related to a primitive and always necessary function, the ingestion of food, as are the sulco-laterals of a planula of *Metridium*.

The characteristic position of the *muscle banners* on the mesenteries of a young Zoantharian might be explained as suitably meeting the needs for protraction and retraction respectively of the "body" and "head" in the creeping ancestor. The need for separation of out-going and in-going currents (respiratory or nutritive) in any large fixed cœlenterate would ensure the retention of bilaterality once acquired.

Colony formation with elongation of the mouth in relation to the axis of an

* A parallel to *chorda formation* from endoderm is found in cœlenterates. One may note that young *Pleurobrachia pileus* are much stiffer along their meridional lines than over the rest of their surface. Sections show that the outer walls of the meridional canals consist in great part of large vacuolated cells presenting a remarkable resemblance to developing notochordal tissue, and that there are two similar but smaller "stiffening" strips in the wall of each paragastric canal where it abuts on the stomodæum. The presence and distribution of vacuolated cells in Ctenophores has, of course, long been known, but in view of the question above referred to, it seems opportune to cite this instance of their close affinity to chorda tissue as regards differentiation and function.

elongated stock, has been put forward by HAACKE (13) as the originating cause of Hexactinian bilaterality, but this explanation seems altogether far-fetched.

When the Zoantharian stock became fixed, a kind of *metamorphosis* would occur, allowing a reduction of the mesenchyme needed in the free condition. A similar reduction might indeed accompany fixation in any coelenterate. This mesenchyme might be utilised for nutritive purposes as occurs, for example, in the metamorphosis of Echinoderms. Reflected forward in present ontogeny the reduction process might furnish a starting-point for the peculiar formation of the *trophenchyme* (pp. 357, 360), and for its passage into or inclusion within the archenteron, and its digestion there. Even in the late metamorphosis of Echinoderms the nutritive material derived from lost larval structures finds its way to the stomach, the walls of which for a time become syncytial and greatly thickened (see *e.g.*, MACBRIDE, 22, GEMMILL, 11). Information regarding the early development of the Zoanthidea would be of much interest since the adults have abundant mesenchyme.

BOURNE (3, and p. 19 of Ctenophora) expresses the view that "the Turbellaria, Nemertines and Ctenophora are descended from a common ancestor," which "would be spherical or hemispherical in shape, and have an aboral sense-organ consisting of a plate of thickened ectoderm provided with long stiff cilia. The line joining mouth and sense-organ would be the chief axis of the body. The digestive tract would consist of a stomodæum and a more or less sacculated endoderm, and would be surrounded by a mesenchymous tissue derived from a special germ layer, the mesoblast. Such an ancestor would itself be . . . very probably a form resembling the early larvæ of Actinians."

The above conditions are strikingly fulfilled in the planula of *Metridium*, except that the "mesoderm" (see p. 353) is too scanty to be called a layer.

It may be added against the hypothesis which derives Turbellarians from Ctenophores (1) that the branched canals (mainly ectodermal, but probably also partly endodermal), characteristic of various Zoanthidea with abundant mesenchyme (HADDON, 16) offer a better comparison with the Platyelmian excretory system than do the aboral tubes of Ctenophores, and that, as SEDGWICK pointed out, marginal pores in Medusæ and cinclide perforations in Actiniæ may be compared with nephridial openings; (2) what is known regarding the development of the Platyctenian Ctenophores indicates that they are modified from distinctively Ctenophoran forms; (3) the Ctenophore-Turbellarian hypothesis risks the initial danger of deriving a lowly phylum from a greatly specialised prototype; (4) the eight ciliated lobes of Müller's Turbellarian larva have an arrangement with reference to the axis of bilaterality which corresponds to that of the eight tentacles of a young Actinian and not to that of the ribs and meridional pouches of Ctenophores; (5) lastly, the resemblance between a *Metridium* larva creeping mouth-downwards (p. 354) and a Turbellarian claims consideration.

IV. ABNORMALITIES.

Double Monsters.—Several of these reached fixation and tentacle formation in my hatching vessels. In all the base was single. In one specimen a larger erect column carried a smaller one coming off at right angles from it near the base. In others the division was more equal and occurred quite near the crown or at a varying distance down the column. In perfect cases the two heads had the full number of tentacles and mesenteries. One triple monster was noted. In this case a column, single at the base, was divided into two, and of these one was again divided. The first head and one of the two other heads were perfect, while the third had only four or five tentacles. A mouth opening was present in each of the three heads. A certain number of young larvæ with two or even three gastrula-invaginations appeared in my early cultures, and there can be no doubt that as in *Luidia* (GEMMILL, 13), the double and triple *Adamsia* monsters developed from such abnormal larvæ.

Experimental.—Separation of single blastomeres in the 4- and 8-celled stages of *Adamsia*, and fragmentation of the preblastula in the same species occur readily when the eggs are shaken. The isolated cells or cell masses tend to develop further, giving rise to tiny swarming larvæ with a mouth and gastric cavity. One late specimen, which had probably developed from a blastomere of the 4-celled stage, when cut into sections showed the two sulco-lateral mesenteries with their stomodæal epiblastic downgrowths. Many Coelenterates exhibit passage of chromatin from the nucleus into the protoplasm and yolk of the growing ova. This process occurs in *Adamsia*, and accordingly we have an argument against the localisation of organ-building substances being necessarily connected with it.

Irregularities of mesenteries.—Apart from double and triple monsters, I came across no late larvæ which varied from the typical 8-mesenteried bilateral symmetry. We may be certain therefore that out of the hosts of young *Metridium* which one finds in suitable localities, a grain of wheat and upwards in size, very few have grown directly from attached planulæ. Examination of their mesenteries gives only the rarest instances in which the arrangement could be derived from a typical 8-mesenteried stage, and comparison of specimens indicates how readily regeneration from a portion of the base containing only a few mesenteries takes place. I have seen a slender specimen ($\frac{3}{8}$ inch long) with only five tentacles and the same number of mesenteries. Healing, formation of a new mouth, and gradual production of new mesenteries occur with great readiness. This kind of reproduction takes place in the Firth of Clyde most abundantly among the small anemones which find attachment to masses of mussels in the lower tidal zone. Perhaps wave action, the irregularity of the spaces between the shells, often bridged by byssus threads, and the sharp edges of the shells may give a greater mechanical stimulus to division than is experienced by anemones living in a smoother and more settled environment.

The process is not so much one of budding as of fragmentation, and this may

explain the remarkable irregularities which have been recorded in the mesenteries of various species of Malacactineæ. Thus PARKER (32) states that out of 131 adult specimens of *Metridium dianthus*, 77 had one, 53 had two, and one had three siphonoglyphs. There is no need to suggest with PARKER that such monoglyphic and diglyphic specimens may be different varieties, or with McMURRICH (25) that a pair of originally directive mesenteries may have become non-directive. PARKER himself refers to the possibility that his irregular specimens may have arisen as buds, while McMURRICH (25) pointed out the absurd situation which would arise if classificatory importance were to be attached to the monoglyphic, or even to the aglyphic, condition taken by itself. PARKER's tryglyphic specimen may have originated from a double monstrosity. We had living at Millport a good-sized double *Metridium*, dredged near the Station, and showing no change whatever for several years, except increase in size. Numerous references to double Anemones occur in literature, and these are usually described as stages in ordinary fission, but I am convinced that stable duplicity of developmental origin may occur in Actinians, as it does in so many other types of animals.

V. SUMMARY.

Segmentation is equal or subequal, total from the first in *Metridium*, beginning with a 4-celled stage in *Adamsia*. There is a bilaminar, greatly folded, and subsequently often saucer-shaped *pre-blastula* stage in *Adamsia*. The blastulæ are spherical, hollow in *Metridium*, but filled in *Adamsia* by a central *non-nucleated* or *sparsely nucleated trophic mass*, produced by constriction of the inner yolky ends of the blastula wall-cells. *Embolic gastrulation*, sometimes assisted by unipolar cell proliferation, occurs in both, and in *Adamsia* the central trophic material gradually passes through the in-pushing endoderm into the cavity of the archenteron. In *Metridium* a small amount of "mesoderm" is formed from the developing endoderm cells. The blastopore becomes the mouth, and in early stages is oval or slit-like and slightly to one side. The larva of *Metridium* has an *aboral tuft* of long cilia and an *aboral sense-organ*. The *stomodæum* forms by in-folding of epiblast at the blastopore, with subsequent elongation by interstitial growth. There is a definite 8-mesenteried stage. The sulco-lateral mesenteries are the first to appear. The *mesenteric filaments* contain down-growths of stomodæal epiblast. The planula is provided with stinging cells. In *Metridium*, prior to aboral fixation and to tentacle formation, *creeping*, mouth-downwards, with stomodæum more or less everted, occurs. Probably *feeding* takes place at this time, as it does during the immediately preceding late planula stage. It is suggested that the Anthozoa acquired an ectodermal stomodæum, and the rudiments of bilateral symmetry during a creeping ancestral stage, from which also the Turbellaria and the Higher Metazoa were derived (p. 363, *et seq.*). The Turbellaria, however, are nearer to the primitive Zoantharian than to the Ctenophoran type (p. 365).

A close comparison is made between the series of primary mesenteric pouches in *Edwardsia* and the coelomic pouches of higher segmented animals (p. 363, *et seq.*). A distinction is drawn between trophenchyme and endoderm in the cell-contents of solid coelenterate planulæ, and a phylogenetic explanation of the presence of the former is hazarded (p. 365). Double monstrosity, irregularities of mesenteries, and production of larvæ from isolated blastomeres or from blastula fragments, are briefly discussed (p. 366).

REFERENCES.

- (1) APPELLÖF, A. "Studien über Aktinien-Entwicklung." 'Bergens Museum, Aarbog.,' I, pp. 1-99 (1900).
- (2) BENEDEN, E. VAN. "Recherches sur le Développement des Arachnactis," 'Archiv Biol.,' vol. 11, pp. 115-146 (see specially p. 120) (1891).
- (2A) *Idem.* "Les Anthozoaires de la Plankton Expédition," 'Ergebnisse der Plankton Expedition der Humboldt Stiftung,' vol. 2, K.e.
- (3) BOURNE, G. C. Article "Anthozoa" in 'Encycl. Brit.,' 11th ed., vol. 2, pp. 99-104.
- (4) BOVERI, TH. "Ueber Entwicklung und Verwandtschaften der Aktinien," 'Zeitschr. Wiss. Zool.,' vol. 49, pp. 461-502 (see specially p. 489) (1890).
- (5) CARLGREN, O. "Ueber die Bedeutung der Flimmerbewegung für die Nahrungstransport bei den Actiniarien und Madreporarien," 'Biol. Centralbl.,' vol. 25, pp. 308-322 (1905).
- (6) *Idem.* "Aktinien-Larven," 'Nordisches Plankton,' 5th Lief., XI, p. 86 (1906).
- (7) CARY, L. R. "The Formation of Germ Layers in *Actinia bermudensis* Verr.," 'Biol. Bull. Woods Hole,' vol. 19, pp. 339-346 (1910).
- (8) DELAGE ET HEROUARD. 'Traité de Zoologie Concrète,' vol. 2, "Coelentères."
- (9) DUERDEN. "West Indian Madreporarian Polyps," 'Memoirs National Acad. Sciences, Washington,' vol. 8 (1902).
- (10) FAUROT, L. "Études sur l'anatome, l'histologie, et le développement des Actinies," 'Arch. Zool. Expér.,' Series 3, vol. 3, pp. 43-262.
- (11) GEMMILL, J. F. "The Development of the Starfish *Solaster endeca*, Forbes," 'Trans. Zool. Soc., London,' pp. 1-71 (1912).
- (11A) *Idem.* "The Development of the Starfish *Asterias rubens*, Linn.," 'Phil. Trans.,' Series B, vol. 205, pp. 213-294 (1914).
- (12) *Idem.* "The Development of the Starfish *Porania pulvillus*, O.F.M.," 'Quart. Journ. Micr. Sc.,' vol. 61, pp. 27-50.
- (13) *Idem.* "Twin Gastrulæ and Bipinnariæ of *Luidia*," 'Journ. Mar. Biol. Ass. U.K.,' vol. 10, pp. 577 *et seq.* (1915).

- (14) HAACKE, W. "Zur Blastologie der Korallen," 'Jenaische Zeitschr.,' vol. 13, pp. 269-320 (1879).
- (15) HAMMAR, J. A. "Ueber eine allgemein vorkommende Protoplasma-verbindung zwischen den Blastomeren," 'Archiv f. Mikr. Anat.,' vol. 49, pp. 92-102.
- (16) HADDON, A. "A Revision of the British Actiniæ. II.—The Zoantheæ." 'Trans. Roy. Dublin Soc.,' Series 2, vol. 4.
- (17) JOURDAN, E. "Recherches Zool. et Histolog. sur les Zoanthaires du Golfe de Marseille," 'Ann. Sc. Nat. Zoologie,' Series 6, vol. 10 (1878).
- (18) KOWALEWSKY, A. See Hoffman u. Schwalbe, 'Jahresber. f. Anat.' (1873).
- (19) LACAZE DUTHIERS, H. "Développement des Coralliaires. Actinaires sans Polypier," 'Arch. Zool. Expér.,' vol. 1 (1872).
- (20) LANG, A. "Die Polycladen des Golfes von Neapel," 'Fauna u. Flora des Golfes von Neapel,' vol. 11 (1899).
- (21) LANKESTER, E. R. 'A Treatise on Zoology. Part II.—Cœlentera' (by G. C. BOURNE).
- (22) MACBRIDE, E. W. "The Development of *Echinus esculentus*," 'Phil. Trans.,' Series B, vol. 195, pp. 235-250.
- (23) *Idem.* 'Text-book of Embryology,' vol. 1—"Invertebrates" (1914).
- (24) McMURRICH, J. P. "On the Development of the Hexactiniæ," 'Journ. Morph.,' vol. 4, pp. 303-330.
- (25) *Idem.* "On some Irregularities in the Number of the Directive Mesenteries in the Hexactiniæ," 'Zoological Bulletin,' vol. 1, pp. 115-122 (1897).
- (26) *Idem.* "Contributions on the Morphology of the Actinozoa. III.—The Phylogeny of the Actinozoa," 'Journ. Morph.,' vol. 5, pp. 125-161.
- (27) MASTERMAN, A. T. "The Theory of Archimeric Segmentation and its Bearing on the Phyletic Classification of the Cœlomata," 'Proc. Roy. Soc., Edinburgh,' vol. 22, pp. 270-310 (1898).
- (28) *Idem.* "The Early Development of *Cribrella oculata* (Forbes), with Remarks on Echinoderm Development," 'Trans. R. Soc. Edin.,' vol. 40, pp. 373-417.
- (29) MATTHEWS, A. "The Development of *Alcyonium digitatum*, with some Notes on the Early Colony Formation," 'Quart. Journ. Micr. Sc.,' vol. 62, pp. 43-94 (1916).
- (30) MORTENSEN, TH. "On the Development of some British Echinoderms," 'Journ. Mar. Biolog. Assoc. U.K.,' vol. 10, pp. 1-18.
- (31) NEWTH, A. G. "The Early Development of Cucumaria: Preliminary Account," 'Proc. Zool. Soc. Lond.,' pp. 631-641 (1916).
- (32) PARKER, G. H. "The Mesenteries and Siphonoglyphs in *Metridium marginatum*, Milne-Edwards." 'Bull. Mus. Comp. Zool. Harvard,' vol. 30, pp. 259-273 (1879).
- (33) SEDGWICK, A. "On the Origin of Metameric Segmentation and some other Morphological Questions," 'Quart. Journ. Micr. Sc.,' vol. 24, pp. 43-82.

- (34) WILSON, E. B. "The Development of *Renilla*," 'Phil. Trans.,' vol. 174, pp. 723-815 (1883).
 (35) WILSON, H. V. "The Development of *Manicina areolata*," 'Journ. Morph. Boston,' vol. 2, pp. 191-252.
 (36) ZOJA. "Sullo sviluppo degli blastomeri isolate delle uova di alcune Meduse," 'Arch. Entwickl. Mech.,' vol. 1, pp. 573-595; vol. 2, pp. 1-37.

EXPLANATION OF FIGURES.

All the illustrations, except Figs. 22-24, are photomicrographs of sections, or of specimens mounted whole.

ABBREVIATIONS EMPLOYED.

ab. cn., aboral pole with stinging threads extruded; *bl.*, blastopore; *bl. c.*, blastula cavity; *ect.*, ectoderm; *end.*, endoderm; *g. c.*, gastric cavity; *mes.*, mesoderm; *nuc. tr.*, nuclei in trophenchyme; *o. cn.*, oral pole with stinging threads extruded; *s.*, a developing mesentery; *s. l.*, sulco-lateral mesenteries; *s. l. f.*, sulco-lateral mesenteries showing epiblastic down-growth from stomodæum for mesenteric filament; *s. 2.*, sulculo-lateral mesenteries; *s. 3.*, sulcar (*future* sulcar directive) mesenteries; *s. 4.*, sulcular (*future* sulcular directive) mesenteries; *s. c.*, saucer cavity; *s. g. c.*, segmentation cavity; *s. or.*, aboral sense-organ; *st.*, stomodæum; *st. 1.*, *st. 2.*, stomodæa of a double specimen; *st. ep.*, epithelium of everted stomodæum; *tr. bl.*, trophenchyme within the blastula; *tr. g.*, trophenchyme within the archenteron or gastric cavity of the planula.

PLATE 58 (*Metridium*).

- Fig. 1.—Egg of *Metridium* recently shed. The small adherent body may be a polar corpuscle.
 Fig. 2.—Two-celled stage.
 Fig. 3.—Four-celled stage.
 Fig. 4.—Stage with ten cells. The cells here are more widely separated than is usual.
 Fig. 5.—Section of corresponding stage (normal) in which the cells are closer.
 Fig. 6.—Sections of early stages. In the right-hand specimen the cells are incompletely separated from one another at their inner ends (see p. 352).
 Fig. 7.—Section of early blastula. The central cavity is slightly larger than is usual at this stage. It will be noted that, here and in fig. 9, the yolky contents are chiefly aggregated towards the inner ends of the cells.
 Fig. 8.—Section of later blastula showing cellular and non-cellular contents in the blastula cavity (see p. 353).

- Fig. 9.—Section of typical fully formed blastula. The thinner-walled slightly swollen region is the future aboral end.
- Fig. 10.—Section of blastula showing commencing invagination of the entoderm. The shape has now altered, the aboral end being more pointed than the oral one.
- Figs. 11, 12.—Sections of slightly later stages in gastrulation, the first chosen as showing a very narrow invagination cavity, while in the second the cavity is more widely patent. Separation of a few cells from the inner aspect of the in-growing part is seen in both cases. These cells are interpreted as being "mesodermal" in character.
- Fig. 13.—Section of later gastrula. A cell thickening is seen at the aboral end—the rudiment of the aboral sense-organ.
- Fig. 14.—Longitudinal section of a young planula.
- Fig. 15.—Longitudinal section of older planula showing the apical tuft of cilia and the cell thickening underneath it. The stomodæum is an open canal. In figs. 12–15 the early tendency for one lip of the blastopore to be slightly more prominent than the other is exhibited.
- Fig. 16.—Longitudinal section of similar planula showing one of the long sulco-lateral mesenteries with its border of ectoderm derived by down-growth from the stomodæum.
- Fig. 17.—View of planula mounted whole, showing the oral and aboral armature of stinging cells with the threads shot out. The aboral end is uppermost, and the dark line down the middle is caused by the thickened sulco-lateral mesenteries.
- Fig. 18.—Transverse section through upper part of gastric cavity of late planula showing the large sulco-lateral mesenteries which divide the cavity into a larger and a smaller compartment.
- Fig. 19.—Transverse section through middle part of gastric cavity of similar planula showing the developing sulco-lateral mesenteries as slight inward projections.
- Fig. 20.—Sections of early blastulæ containing in their central cavities a greater than normal amount of cellular and non-cellular material.
- Fig. 21.—Attempt at gastrulation in a larva having its central cavity filled with cellular and non-cellular material. These larvæ, while abnormal, may be of interest as throwing light on the mode of entoderm formation in certain other species which do not exhibit a hollow blastula stage.
- Fig. 22.—Diagram of longitudinal section of larva (at stage represented in fig. 16), passing through the sulco-lateral mesenteries on either side, and showing also the stomodæum and gastric cavity. The downward extension of stomodæal epiblast on the surface of the mesenteries is indicated by the black line.

Fig. 23.—Diagram of transverse section through upper part of gastric cavity of a slightly older specimen than that shown in fig. 18. The black line on the surface of the sulco-lateral mesenteries (s. 1) marks the downward extension of stomodæal epiblast. The first indication of the sulculo-lateral (s. 2), the sulcar (s. 3), and the sulcular (s. 4) mesenteries is also shown.

Fig. 24.—Diagram of the late larva, in longitudinal section, at stage of oral fixation and creeping. The stomodæum is everted, bringing the oral ends of the sulco-lateral mesenteries into contact with the substratum.

PLATE 59, Figs. 25–62; (*Adamsia*).

Fig. 25.—Egg immediately after shedding.

Fig. 26.—Four-celled stage (3 hours).

Fig. 27.—Early morula (5 hours).

Fig. 28.—Later morula (characteristically irregular; photographed as an opaque object; 10 hours).

Fig. 29.—A group of morulæ, pre-blastulæ and blastulæ (photographed as opaque objects; 6–30 hours).

Fig. 30.—Pre-blastula (crumpled disc) stage under higher magnification (15 hours).

Figs. 31, 32.—Early saucer pre-blastula stages (the latter photographed as an opaque object; 18 hours).

Figs. 33.—Late saucer stage; the remnant of the saucer cavity is seen faintly in the centre being now almost completely filled up (24 hours) (*cf.* figs. 54, 55).

Fig. 34.—Typical smooth blastula (photographed as an opaque object).

Fig. 35.—Late blastula with flattening at one end where gastrulation will take place. In this specimen the small notch on the right side still marks the remnant of the saucer opening. The darker central area is non-nucleated trophic reticulum (30 hours) (*cf.* fig. 60).

Figs. 36, 37.—Commencement of gastrulation (30–36 hours). The prominent lip of the blastopore (see p. 357) is on the left side in fig. 36, and uppermost (*i.e.*, towards the microscope) in fig. 37.

Fig. 38.—Stage similar to the last two (36 hours), but still showing remnant of saucer opening as a slight dimple (photographed as an opaque object).

Figs. 39–42.—Stages in gastrulation (48–72 hours).

Fig. 43.—Fully formed planula (84 hours). There is marked elongation: the stomodæum is still relatively short.

Fig. 46.—Older larva ($4\frac{1}{2}$ days) in side view with oral extremity at upper side of figure. The dark streak down the middle is caused by one of the two sulco-lateral mesenteries.

- Fig. 45.—Similar stage viewed from oral end and focussed so as to show the two sulco-lateral mesenteries projecting inwards.
- Fig. 46.—Slightly older stage (six days), viewed from oral end and focussed so as to show the eight primary mesenteries.
- Fig. 47.—Young anemone (a week after fixation : 13 days) with the eight tentacles expanded.
- Fig. 48.—Section of freshly spawned egg showing the finely granular contents, rather clearer in the centre. The thin egg membrane is slightly separated at several points.
- Fig. 49.—Section through early morula showing some flattening and formation of a central cavity.
- Fig. 50.—Section through slightly later morula (10 hours) showing irregularity of outline.
- Fig. 51.—Section through an early pre-blastula (15 hours), crumpled disc stage.
- Figs. 52, 53.—Sections through similar or slightly later (18 hours) pre-blastulae in which the edge of the bilaminar disc is upturned all round in cup- or saucer-like form.
- Fig. 54.—Section through late pre-blastula (24 hours). Filling up of the saucer cavity and formation of the central trophic reticulum are in progress.
- Fig. 55.—Longitudinal section through a blastula (30 hours) in which the last-named processes are practically completed, only a slight dimple on one side remaining to mark the former position of the saucer opening. The central trophic reticulum in this specimen, as in the best blastulae, contains no nuclei.
- Fig. 56.—Transverse section of a blastula of similar age (30 hours), showing a group of nucleated corpuscles near its centre (see p. 357).
- Figs. 57, 58.—Portions of sections of pre-blastula (18 hours) under medium and higher magnification, illustrating mode of formation of the central trophic reticulum. Clear vesicles, with a wall of protoplasm but without nuclei, are being partially separated off from the inner ends of the cells and pushed into the central cavity, which in this case is relatively large.
- Fig. 59.—High power view of portion of blastula at stage shown in fig. 55. The nuclei are all near the free surface, the deeper zone being non-nucleated trophic reticulum.
- Fig. 60.—Longitudinal section of late blastula (36 hours). The commencement of gastrulation is indicated by flattening of one end with proliferation and in-pushing of cells there.
- Fig. 61.—Early stage in gastrulation (48 hours). The cavity of the archenteron gradually fills up with the trophic material which passes through the hypoblast from the interior of the blastula ($\times 120$). (The section does not pass quite through the apex of the aboral pole.)

Fig. 62.—Middle stage in gastrulation (64 hours), showing elongation of the larva and further sinking in of the archenteron.

PLATE 60 (Figs. 63–71) (*Adamsia*).

Fig. 63.—Longitudinal section of late planula showing stomodæum and gastric cavity. The surface of the larva is covered with shot-out stinging threads.

Fig. 64.—Longitudinal section of similar stage. The section passes along the whole length of the epiblastic (mesenteric filament) edge of the two sulco-lateral mesenteries.

Fig. 65.—Transverse section of planula at same stage as fig. 64, the section passing through the main portion of the gastric cavity. The trophic material of the larva is now inside the gastric cavity.

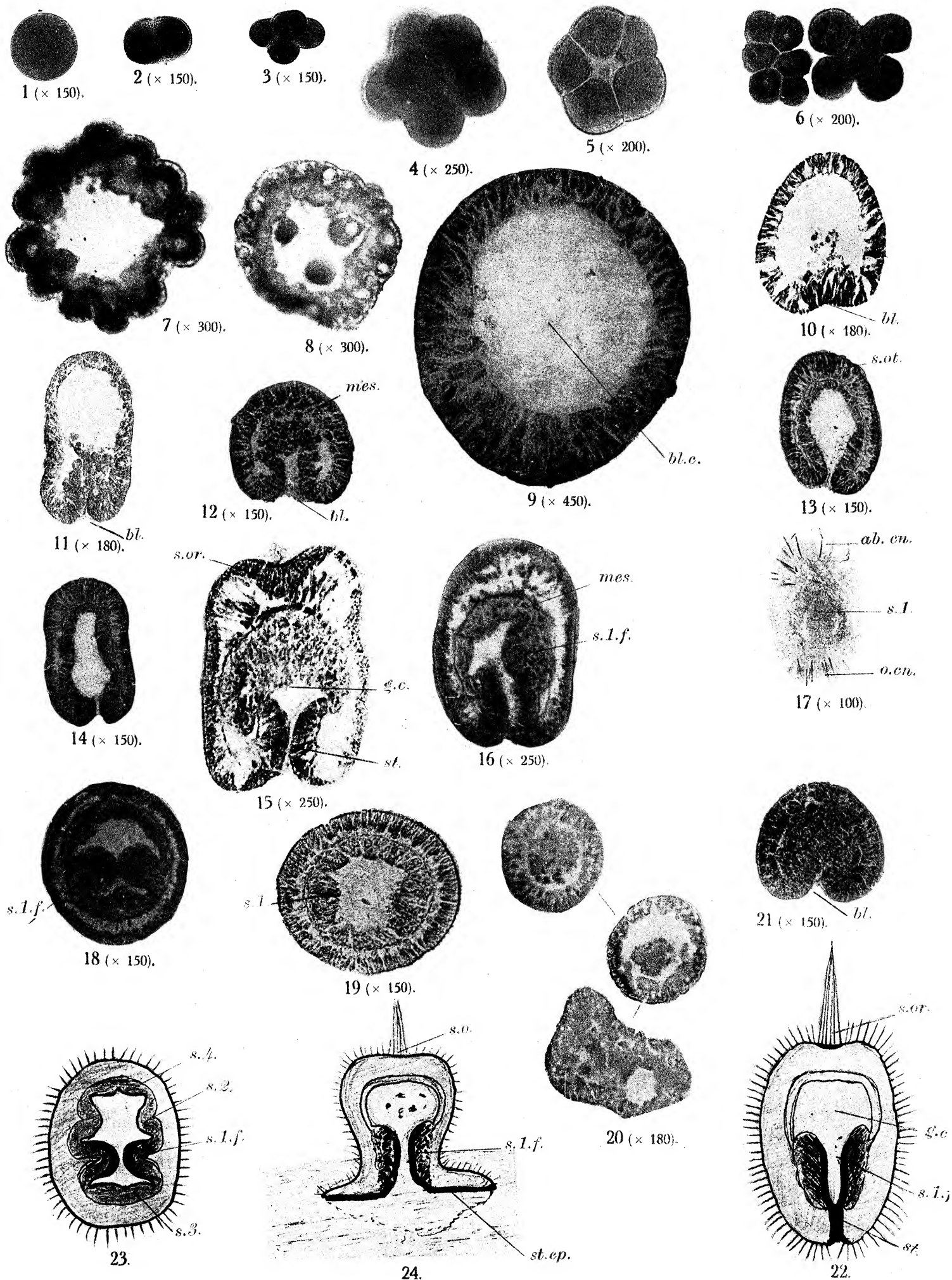
Fig. 66.—High power view in longitudinal section of oral end of a larva at time when down-growth of stomodæal epithelium to form a mesenteric filament is in progress. This down-growth is seen on the right side of the figure, the mesentery concerned being a sulco-lateral one. On the left side the section passes only through stomodæum.

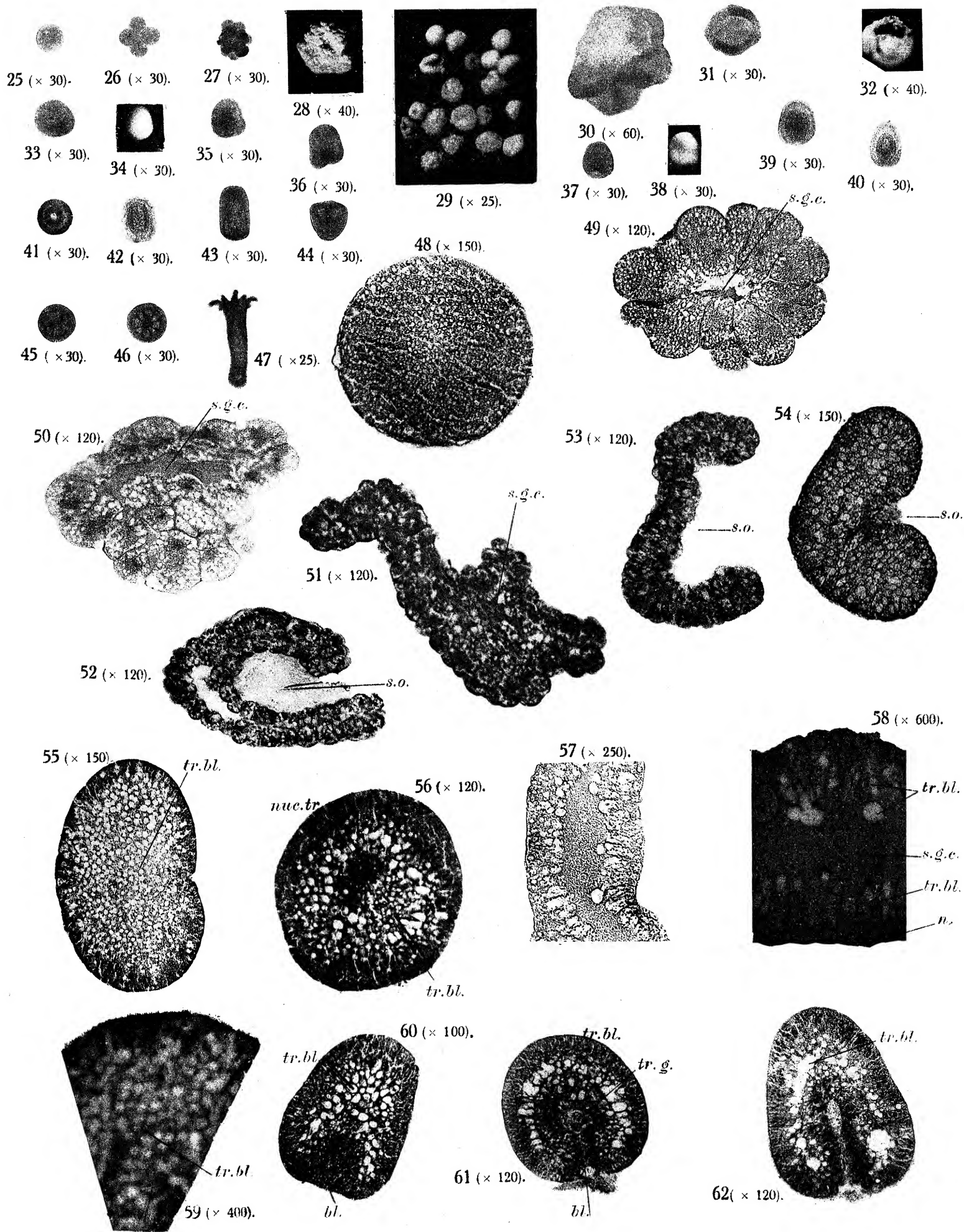
Fig. 67.—Almost longitudinal section of late larva ready for attachment. The superficial involution at \times is not stomodæum but part of the future peristomial area tucked in owing to contraction of the larva when brought into the preserving fluid. On the right side of the figure, one of the sulco-lateral mesenteries with the mesenteric filament border from the stomodæal epiblast is cut along its whole length; on left side of figure the section cuts stomodæum and gastric cavity only.

Fig. 68.—Transverse section through gastric cavity of a larva slightly younger than that shown in fig. 66. The central trophic material, the two sulco-lateral mesenteries, each with a mesenteric filament border, and rudiments of other developing mesenteries are shown.

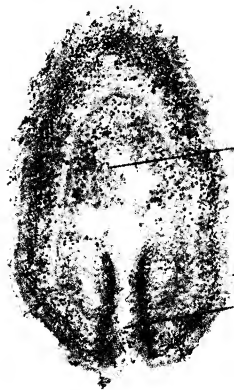
Fig. 69.—Aoral end of a larva similar to the stage illustrated in fig. 67, seen in longitudinal section. The greatly elongated ectoderm, the irregular entoderm with nuclei at various depths, and the fibrillar couch containing a few mesodermic nuclei between ectoderm and entoderm are shown. Fibres, probably muscular and sensory, from this couch are seen passing out into the ectoderm.

Fig. 70.—Transverse section near oral end of an attached stage (*cf.* Plate 59, fig. 47), showing the eight primary mesenteries. A little higher up in this series (*i.e.*, nearer the mouth), the sulcular mesenteries are complete like the rest.





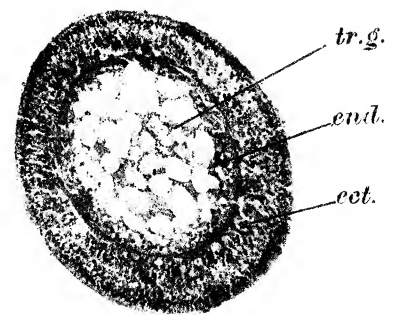
63 ($\times 100$).



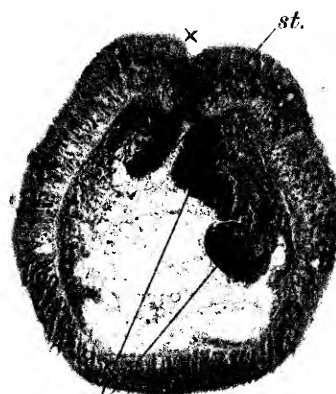
64 ($\times 100$).



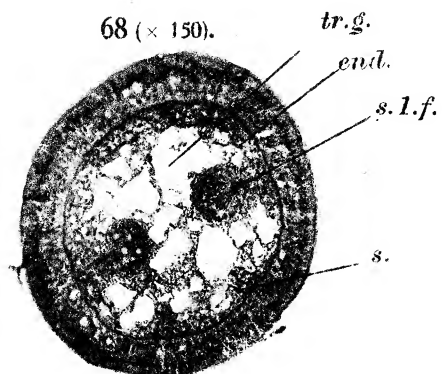
65 ($\times 150$).



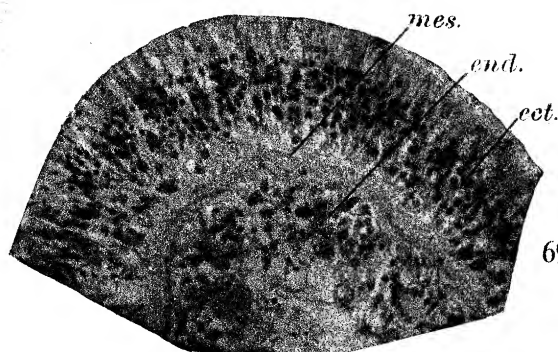
66 ($\times 350$).



67 ($\times 120$).

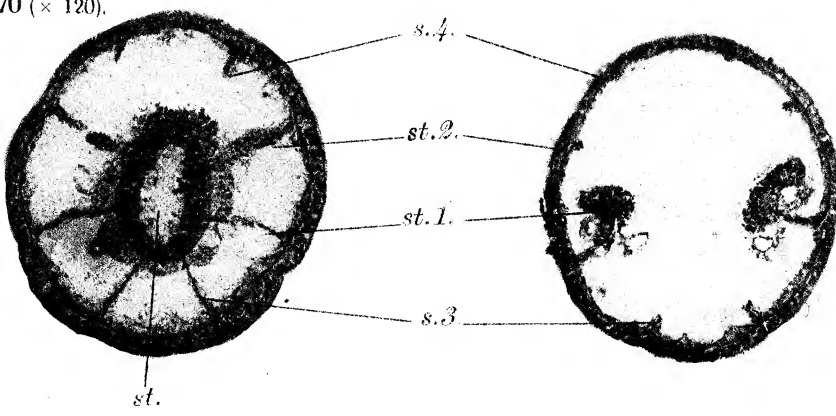


68 ($\times 150$).



69 ($\times 400$).

70 ($\times 120$).



71 ($\times 120$).



72 ($\times 120$).

Fig. 71.—Transverse section through middle of gastric cavity in same specimen as last. The sulco-lateral mesenteries are the only ones which have as yet received a “mesenteric filament” border.

Fig. 72.—Section through a young double-monster anemone of same age as that shown in last figure. The section passes obliquely through the mouth of one of the heads and transversely through the stomodæum of the other. The base was single. Corresponding mesenteries came together and became fused at the region of transition from the double to the single condition.



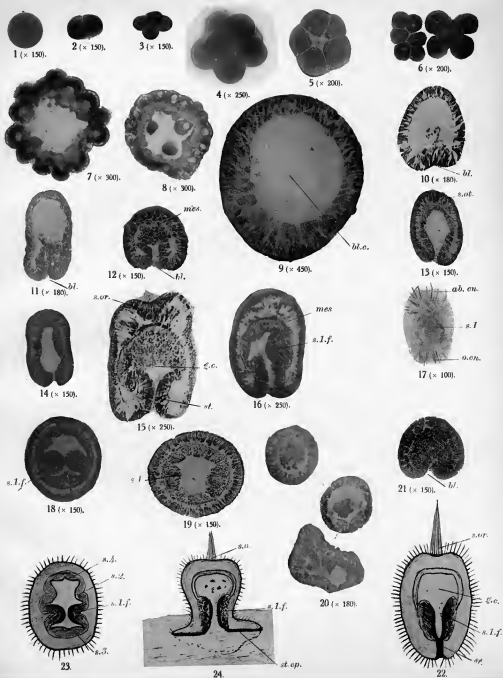


PLATE 58 (*Metridium*).

Fig. 1.—Egg of *Metridium* recently shed. The small adherent body may be a polar corpuscle.

Fig. 2.—Two-celled stage.

Fig. 3.—Four-celled stage.

Fig. 4.—Stage with ten cells. The cells here are more widely separated than is usual.

Fig. 5.—Section of corresponding stage (normal) in which the cells are closer.

Fig. 6.—Sections of early stages. In the right-hand specimen the cells are incompletely separated from one another at their inner ends (see p. 352).

Fig. 7.—Section of early blastula. The central cavity is slightly larger than is usual at this stage. It will be noted that, here and in fig. 9, the yolk contents are chiefly aggregated towards the inner ends of the cells.

Fig. 8.—Section of later blastula showing cellular and non-cellular contents in the blastula cavity (see p. 353).

Fig. 9.—Section of typical fully formed blastula. The thinner-walled slightly swollen region is the future aboral end.

Fig. 10.—Section of blastula showing commencing invagination of the entoderm. The shape has now altered, the aboral end being more pointed than the oral one.

Figs. 11, 12.—Sections of slightly later stages in gastrulation, the first chosen as showing a very narrow invagination cavity, while in the second the cavity is more widely patent. Separation of a few cells from the inner aspect of the in-growing part is seen in both cases. These cells are interpreted as being "mesodermal" in character.

Fig. 13.—Section of later gastrula. A cell thickening is seen at the aboral end—the rudiment of the aboral sense-organ.

Fig. 14.—Longitudinal section of a young planula.

Fig. 15.—Longitudinal section of older planula showing the apical tuft of cilia and the cell thickening underneath it. The stomodaeum is an open canal. In figs. 12-15 the early tendency for one lip of the blastopore to be slightly more prominent than the other is exhibited.

Fig. 16.—Longitudinal section of similar planula showing one of the long sulco-lateral mesenteries with its border of ectoderm derived by down-growth from the stomodaeum.

Fig. 17.—View of planula mounted whole, showing the oral and aboral armature of stinging cells with the threads shot out. The aboral end is uppermost, and the dark line down the middle is caused by the thickened sulco-lateral mesenteries.

Fig. 18.—Transverse section through upper part of gastric cavity of late planula showing the large sulco-lateral mesenteries which divide the cavity into a larger and a smaller compartment.

Fig. 19.—Transverse section through middle part of gastric cavity of similar planula showing the developing sulco-lateral mesenteries as slight inward projections.

Fig. 20.—Sections of early blastulae containing in their central cavities a greater than normal amount of cellular and non-cellular material.

Fig. 21.—Attempt at gastrulation in a larva having its central cavity filled with cellular and non-cellular material. These larvae, while abnormal, may be of interest as throwing light on the mode of entoderm formation in certain other species which do not exhibit a hollow blastula stage.

Fig. 22.—Diagram of longitudinal section of larva (at stage represented in fig. 16), passing through the sulco-lateral mesenteries on either side, and showing also the stomodaeum and gastric cavity. The downward extension of stomodaeal epiblast on the surface of the mesenteries is indicated by the black line.

Fig. 23.—Diagram of transverse section through upper part of gastric cavity of a slightly older specimen than that shown in fig. 18. The black line on the surface of the sulco-lateral mesenteries (*s.1*) marks the downward extension of stomodaeal epiblast. The first indication of the sulco-lateral (*s.2*), the sulcar (*s.3*), and the sulcular (*s.4*) mesenteries is also shown.

Fig. 24.—Diagram of the late larva, in longitudinal section, at stage of oral fixation and creeping. The stomodaeum is everted, bringing the oral ends of the sulco-lateral mesenteries into contact with the substratum.

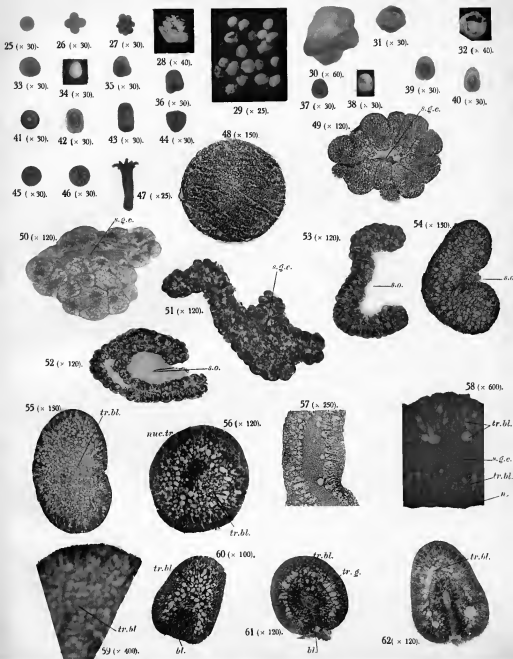


PLATE 59, Figs. 25-62; (*Adamsia*).

- Fig. 25.—Egg immediately after shedding.
 Fig. 26.—Four-celled stage (3 hours).
 Fig. 27.—Early morula (5 hours).
 Fig. 28.—Later morula (characteristically irregular; photographed as an opaque object; 10 hours).
 Fig. 29.—A group of morulae, pre-blastulae and blastulae (photographed as opaque objects; 6-30 hours).
 Fig. 30.—Pre-blastula (crumpled disc) stage under higher magnification (15 hours).
 Figs. 31, 32.—Early saucer pre-blastula stages (the latter photographed as an opaque object; 18 hours).
 Figs. 33.—Late saucer stage; the remnant of the saucer cavity is seen faintly in the centre being now almost completely filled up (24 hours) (cf. figs. 54, 55).
 Fig. 34.—Typical smooth blastula (photographed as an opaque object).
 Fig. 35.—Late blastula with flattening at one end where gastrulation will take place. In this specimen the small notch on the right side still marks the remnant of the saucer opening. The darker central area is non-nucleated trophic reticulum (30 hours) (cf. fig. 60).
 Figs. 36, 37.—Commencement of gastrulation (30-36 hours). The prominent lip of the blastopore (see p. 357) is on the left side in fig. 36, and uppermost (i.e., towards the microscope) in fig. 37.
 Fig. 38.—Stage similar to the last two (36 hours), but still showing remnant of saucer opening as a slight dimple (photographed as an opaque object).
 Figs. 39-42.—Stages in gastrulation (48-72 hours).
 Fig. 43.—Fully formed planula (84 hours). There is marked elongation: the stomodaeum is still relatively short.
 Fig. 46.—Older larva ($4\frac{1}{2}$ days) in side view with oral extremity at upper side of figure. The dark streak down the middle is caused by one of the two sulco-lateral mesenteries.
 Fig. 45.—Similar stage viewed from oral end and focussed so as to show the two sulco-lateral mesenteries projecting inwards.
 Fig. 46.—Slightly older stage (six days), viewed from oral end and focussed so as to show the eight primary mesenteries.
 Fig. 47.—Young anemone (a week after fixation: 13 days) with the eight tentacles expanded.
 Fig. 48.—Section of freshly spawned egg showing the finely granular contents, rather clearer in the centre. The thin egg membrane is slightly separated at several points.
 Fig. 49.—Section through early morula showing some flattening and formation of a central cavity.
 Fig. 50.—Section through slightly later morula (10 hours) showing irregularity of outline.
 Fig. 51.—Section through an early pre-blastula (15 hours), crumpled disc stage.
 Figs. 52, 53.—Sections through similar or slightly later (18 hours) pre-blastulae in which the edge of the bilaminar disc is upturned all round in cup- or saucer-like form.
 Fig. 54.—Section through late pre-blastula (24 hours). Filling up of the saucer cavity and formation of the central trophic reticulum are in progress.
 Fig. 55.—Longitudinal section through a blastula (30 hours) in which the last-named processes are practically completed, only a slight dimple on one side remaining to mark the former position of the saucer opening. The central trophic reticulum in this specimen, as in the best blastulae, contains no nuclei.
 Fig. 56.—Transverse section of a blastula of similar age (30 hours), showing a group of nucleated corpuscles near its centre (see p. 357).
 Figs. 57, 58.—Portions of sections of pre-blastula (18 hours) under medium and higher magnification, illustrating mode of formation of the central trophic reticulum. Clear vesicles, with a wall of protoplasm but without nuclei, are being partially separated off from the inner ends of the cells and pushed into the central cavity, which in this case is relatively large.
 Fig. 59.—High power view of portion of blastula at stage shown in fig. 55. The nuclei are all near the free surface, the deeper zone being non-nucleated trophic reticulum.
 Fig. 60.—Longitudinal section of late blastula (36 hours). The commencement of gastrulation is indicated by flattening of one end with proliferation and in-pushing of cells there.
 Fig. 61.—Early stage in gastrulation (48 hours). The cavity of the archenteron gradually fills up with the trophic material which passes through the hypoblast from the interior of the blastula ($\times 120$). (The section does not pass quite through the apex of the aboral pole.)
 Fig. 62.—Middle stage in gastrulation (64 hours), showing elongation of the larva and further sinking in of the archenteron.

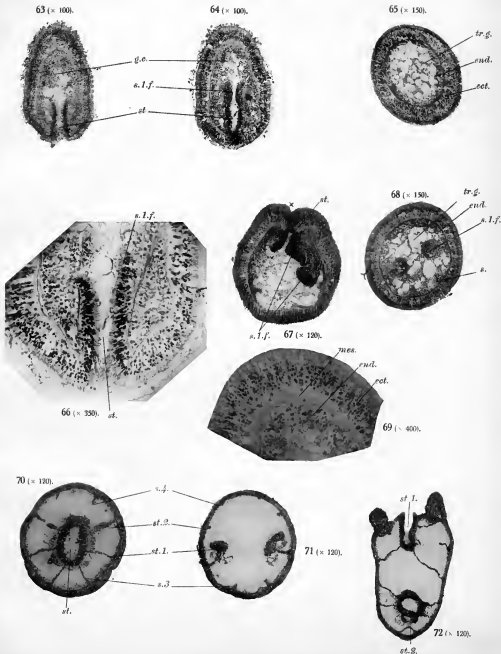


PLATE 60 (Figs. 63-71) (*Adamsia*).

- Fig. 63.—Longitudinal section of late planula showing stomodæum and gastric cavity. The surface of the larva is covered with shot-out stinging threads.
- Fig. 64.—Longitudinal section of similar stage. The section passes along the whole length of the epiblastic (mesenteric filament) edge of the two sulco-lateral mesenteries.
- Fig. 65.—Transverse section of planula at same stage as fig. 64, the section passing through the main portion of the gastric cavity. The trophic material of the larva is now inside the gastric cavity.
- Fig. 66.—High power view in longitudinal section of oral end of a larva at time when down-growth of stomodæal epithelium to form a mesenteric filament is in progress. This down-growth is seen on the right side of the figure, the mesentery concerned being a sulco-lateral one. On the left side the section passes only through stomodæum.
- Fig. 67.—Almost longitudinal section of late larva ready for attachment. The superficial involution at \times is not stomodæum but part of the future peristomial area tucked in owing to contraction of the larva when brought into the preserving fluid. On the right side of the figure, one of the sulco-lateral mesenteries with the mesenteric filament border from the stomodæal epiblast is cut along its whole length; on left side of figure the section cuts stomodæum and gastric cavity only.
- Fig. 68.—Transverse section through gastric cavity of a larva slightly younger than that shown in fig. 66. The central trophic material, the two sulco-lateral mesenteries, each with a mesenteric filament border, and rudiments of other developing mesenteries are shown.
- Fig. 69.—Aboral end of a larva similar to the stage illustrated in fig. 67, seen in longitudinal section. The greatly elongated ectoderm, the irregular endoderm with nuclei at various depths, and the fibrillar couch containing a few mesodermic nuclei between ectoderm and endoderm are shown. Fibres, probably muscular and sensory, from this couch are seen passing out into the ectoderm.
- Fig. 70.—Transverse section near oral end of an attached stage (*cf.* Plate 59, fig. 47), showing the eight primary mesenteries. A little higher up in this series (*i.e.*, nearer the mouth), the sulcular mesenteries are complete like the rest.
- Fig. 71.—Transverse section through middle of gastric cavity in same specimen as last. The sulco-lateral mesenteries are the only ones which have as yet received a "mesenteric filament" border.
- Fig. 72.—Section through a young double-monster anemone of same age as that shown in last figure. The section passes obliquely through the mouth of one of the heads and transversely through the stomodæum of the other. The base was single. Corresponding mesenteries came together and became fused at the region of transition from the double to the single condition.